2016

# Ecosystem Services Provided by Avian Scavengers

Travis L. DeVault
*USDA/APHIS/WS National Wildlife Research Center*, Travis.L.DeVault@aphis.usda.gov

James C. Beasley
*University of Georgia*, beasley@srel.uga.edu

Zachary H. Olson
*University of New England*, zolson@une.edu

Marcos Moleón
*Universidad Miguel Hernández*, mmoleonpaiz@hotmail.com

Martina Carrete
*Universidad Pablo de Olavide, Sevilla*, martina@ebd.csic.es

***See next page for additional authors***

**Authors**
Travis L. DeVault, James C. Beasley, Zachary H. Olson, Marcos Moleón, Martina Carrete, Antoni Margalida, and José Antonio Sánchez-Zapata

# Ecosystem Services Provided by Avian Scavengers

**Published in:**
*Why Birds Matter: Avian Ecological Function and Ecosystem Services.* C.H. Şekercioğlu, D.G. Wenny, and C.J. Whelan, eds. University of Chicago Press, Chicago, IL, USA. 2016. p.235-270.

**Author affiliations:**

Travis L. DeVault,
USDA APHIS Wildlife Services, NWRC, Sandusky
travis.l.devault@aphis.usda.gov

James Beasley,
Savannah River Ecology Laboratory, University of Georgia
beasley@srel.uga.edu

Zachary H. Olson,
University of New England
zolson@une.edu

Marcos Moleón,
Universidad Miguel Hernández
mmoleonpaiz@hotmail.com

Martina Carrete,
Universidad Pablo de Olavide, Sevilla
martina@ebd.csic.es

Antoni Margalida,
Universität Bern
antoni.margalida@iee.unibe.ch

José Antonio Sánchez-Zapata,
Universidad Miguel Hernández
toni@umh.es

CHAPTER EIGHT

# Ecosystem Services Provided by Avian Scavengers

Travis L. DeVault, James C. Beasley, Zachary H. Olson, Marcos Moleón, Martina Carrete, Antoni Margalida, and José Antonio Sánchez-Zapata

Food webs developed under classical theoretical models often depict simplistic interactions among trophic levels linked by predation (Hairston et al. 1960). As a result, extensive research efforts have been devoted to studying predator-prey interactions, often ignoring the contribution of scavenging in food-web dynamics. However, recent advancements in food-web theory have recognized the widespread and critical role that scavenging plays in stabilizing food webs in ecosystems throughout the world, thus suggesting that previous models may have greatly underestimated the importance of scavenging in food web research (Wilson and Wolkovich 2011; Barton et al. 2013). Such disregard for the importance of scavenging likely stems from a number of factors, such as human aversion to decomposing matter, difficulties in identifying scavenged versus depredated materials, and the fact that most species utilize carrion opportunistically (DeVault et al. 2003). Nonetheless, recent population declines of a number of obligate scavengers (e.g., vultures) have drawn international attention to this important group of species, and have sparked a renaissance in research on scavenging (Koenig 2006; Sekercioglu 2006; Ogada et al. 2012a; Moleón and Sanchez-Zapata 2015; Buechley and Şekercioğlu 2016a, 2016b; Ogada et al. 2016).

## Carrion as a Unique Food Source

From the perspective of the predator-scavenger, carrion differs from live prey in several ways. At any point in time, there is usually more live prey in an area than there is carrion, because carrion is generally assimilated very quickly after an animal dies, either by decomposition or scavenging (DeVault et al. 2003). Thus, although carrion could be harder to find (although its presence, odor, is often advertised by microbial decomposers; Janzen 1977; Putman 1983; DeVault et al. 2004; Shivik 2006), it is easier to consume than live prey, as it does not bother to hide or defend itself from predators (Moleón et al. 2014b). However, there are risks associated with consuming carrion, as microbial decomposers produce objectionable and dangerous chemicals in their attempt to sequester the resource (Janzen 1977; Burkepile et al. 2006; see Moleón et al. 2015 for further differences between predation and scavenging networks).

Even though carrion is generally scarce compared to live prey, a central question in scavenging ecology concerns carrion availability—that is, how many animals in a given area die in such a way that they become available to scavengers (DeVault et al. 2003). Houston (1979) argued that scavengers (e.g., vultures) obtain very little food from predator-killed animals, because predators either consume all of their prey or guard their kills. In such cases, scavengers must rely on carcasses from animals that die from causes other than natural predation (Pereira et al. 2014). Numerous studies of cause-specific mortality suggest that in many areas a high percentage of animals die from malnutrition, disease, exposure, collision with vehicles and anthropogenic structures, and hunting by humans (when some animal remains are left in the field), and thereby become available to scavengers, although this percentage varies widely across habitats and animal communities (see DeVault et al. 2003). In the Pyrenees, the estimated proportion of carcasses of wild and domestic ungulates available to avian scavengers ranged between 25 and 80%, depending on the habitat occupied by the prey species (forest or open landscape; Margalida et al. 2011a; Margalida and Colomer 2012).

Occasionally carcasses become available to scavengers in spatial and temporal pulses (Wilson and Wolkovich 2011). For example, several species of birds and mammals depend on salmon carcasses when they become available in fall and winter after spawning (Hewson 1995; Ben-David et al. 1997). Brown bears (*Ursus arctos*) and other carnivores extensively scavenge ungulates killed by wild fires in the western United States (Singer et al. 1989; Blanchard and Knight 1990). Also, in some areas domestic carrion (i.e., dead farm animals) provides an important source of food (Lambertucci et al. 2009). Margalida et al. (2011a) showed that in the pre-Pyrenees region of northeastern Spain, wild ungulates do not currently provide enough food to sustain avian scavengers, and domestic animal carcasses are necessary to prevent population declines. Other studies suggest that predator-killed animals are important to scavengers (e.g., Paquet 1992; Wilmers et al. 2003a, b; Selva et al. 2005). For example, Krofel et al. (2012) showed that brown bears often usurp lynx (*Lynx lynx*) kills, thus causing substantial shifts in lynx foraging patterns.

Irrespective of the cause, it is clear that upon death a sufficient number of animals become available to scavengers, which profoundly impact ecosystems (Wilson and Wolkovich 2011; Barton et al. 2013). Houston (1979) suggested that only about 30% of large ungulates in the Serengeti are killed by predators; the rest die from other causes and become available to scavengers. Moreover, Putman (1976) calculated that about 40% of the production of small mammals becomes available to scavengers (see also DeVault et al. 2003). However, these figures vary widely among seasons and regions (Pereira et al. 2014), and many questions remain regarding the availability of wildlife carrion. For example, more information is needed on how differently sized carcasses contribute to the total carrion pool (Barton et al. 2013). Similarly, it is especially difficult to determine how much available biomass within a carcass has been scavenged versus how much has been decomposed (Putman 1983). In the case of osteophagus species, such as the bearded vulture (*Gypaetus barbatus*), some bones evidently are avoided, as is suggested by their accumulation in nests and ossuaries. In this case, bone nutritive value (fat content) and handling efficiency, regardless of bone size and morphology, appear to play an important role in bone selection, because this implies an optimization of foraging time and of the increased energy gained from the food (Margalida 2008a, b).

## The Consumers: Obligate and Facultative Scavengers

Defined broadly, a scavenger is any organism that feeds on a dead animal it did not kill. There is substantive evidence from the literature to suggest that most carnivorous animals will capitalize on carrion resources if given the opportunity (reviewed in DeVault et al. 2003; Pereira et al. 2014; Mateo-Tomás et al. 2015). For example, carcasses in terrestrial (Tabor et al. 2005; Selva et al. 2005) and marine ecosystems (Smith and Baco 2003)

FIGURE 8.1. African vultures on an elephant carcass. Wherever they are still present, social *Gyps* vultures are the dominant avian scavengers of medium to large vertebrate carcasses in the Old World. This photograph, taken by an automatic camera in the Hluhluwe-iMfolozi Park (South Africa), shows a group of white-backed vultures (*G. africanus*) feeding on an elephant (*Loxodonta africana*) carcass. Other avian scavengers, such as white-headed vultures (*Aegypius occipitalis*) and pied crows (*Corvus albus*), are relegated to a marginal role. Photo by Marcos Moleón.

can host several hundred species of invertebrate scavengers (Beasley et al. 2012). Thus, the diversity of organisms considered to be scavengers is large, but the extent to which each of these species uses carrion varies tremendously (DeVault et al. 2003).

Species that scavenge can be separated into two unequal groups. The first group, the obligate scavengers, relies on carrion for its survival and reproduction. The only known terrestrial vertebrates in this group are vultures (both Old- and New-World; figs. 8.1 and 8.2). In fact, due to energetic constraints, obligate vertebrate scavengers must be large soaring fliers (Ruxton and Houston 2004a).

Obligate scavengers as a group exhibit several adaptations that foster their ability to use carrion as a food source. First, they must possess efficient locomotion (Ruxton and Houston 2004a; Shivik 2006). Efficient travel allows obligate scavengers to increase their search area, effectively exchanging the spatial and temporal unpredictability of carrion at local scales for relatively predictable occurrences at much larger scales (DeVault et al. 2003; Ruxton and Houston 2004a). Second, obligate scavengers must be able to find carcasses from great distances, a feat accomplished using keenly focused senses of sight or smell (Houston 1979; DeVault et al. 2003). For example, the obligate scavenging turkey vulture (*Cathartes aura*; fig. 8.3) and congeners possess an excellent olfactory sense (Stager 1964). Finally, obligate scavengers must exhibit morphological and physiological adaptations to the problems encountered when feeding on carcasses. The obligate scavenging vultures have highly acidic stomachs (as low as pH = 1) that probably help to decrease the pathogenic risk of high microbial loads (Houston and Cooper 1975), and few to no feathers on their heads, which reduces fouling (Houston 1979). Thus, obligate scavengers have evolved to efficiently find and acquire the nutrients in carcasses.

FIGURE 8.2. Of the New World vultures, the black (*Coragyps atratus*) and turkey (*Cathartes aura*) vulture are the most widely distributed, and they overlap extensively in range. This photograph, taken by an automatic remote camera in South Carolina, shows a group of black and turkey vultures feeding on a feral pig (*Sus scrofa*) carcass. Although both species are often found using the same carrion resources in areas where they occur sympatrically, black vultures generally are more social and rely primarily on their vision to detect carrion, whereas turkey vultures are less gregarious and have well-developed olfactory capabilities. Photo by James C. Beasley.

FIGURE 8.3. Turkey vultures are abundant across much of North and South America, and are well adapted to human-dominated landscapes. Photo by Travis L. DeVault.

Facultative scavengers, on the other hand, comprise much more diversity than exists among obligate scavengers, as they include all species that scavenge when opportunities arise, but do not depend solely on carrion for survival and reproduction (figs. 8.4 and 8.5). Facultative scavengers exhibit a range in the frequency with which they are associated with scavenging activity (Pereira et al. 2014; Moreno-Opo et al. 2016). For example, carrion feeding is often listed in food-habits descriptions of natural history accounts for generalist species such as the red fox and members of the Corvidae family (McFarland et al. 1979). However, it is less frequently acknowledged that scavenging is also observed among the more specialist predators (e.g., *Buteo* hawks and buzzards, Errington and Breckenridge 1938; various snakes, DeVault and Krochmal 2002; owls, Kapfer et al. 2011), and even among herbivores (e.g., hippopotamus [*Hippopotamus amphibius*]; Dudley 1996). Many facultative scavengers (e.g., raptors; Sánchez-Zapata et al. 2010; Moreno-Opo et al. 2016) eat more carrion than is often assumed, largely because traditional pellet- and prey-remains analysis underrepresents the presence of carrion in their diets (DeVault et al. 2003). It is tempting to view the different frequencies of scavenging

FIGURE 8.4. The golden eagle (*Aquila chrysaetos*) is a facultative avian scavenger with a wide distribution in the Northern Hemisphere. Photo by Eugenio Noguera.

FIGURE 8.5. The African fish-eagle (*Haliaeetus vocifer*) is a specialized fish eater, but it does not pass by opportunities to feed on the small carcasses of both aquatic and terrestrial vertebrates, especially when it is young. Photo by David Carmona.

observed among facultative scavengers as relating directly to each species' general preferences for carrion relative to live prey. However, such differences are more often dependent on the tolerance for the by-products of microbial decomposition and, even more important, the ability to detect and acquire carrion (Janzen 1977; Houston 1979; Shivik 2006).

## Implications of Avian Scavenging for Ecosystems and Humans

### *What Happens to Food Webs when Avian Scavengers Are Removed from Ecosystems?*

Understanding the role of avian scavengers in food webs and ecosystem functioning is indispensable to adequately recognizing the regulating and cultural services that these birds provide to humanity, as well as the supporting services behind them (Moleón et al. 2014a, 2014b). As seen above, carrion represents a vast reservoir of nutrients and energy, and a huge number of bird species (among many other vertebrates, invertebrates, and microorganisms) show adaptations and/or abilities to exploit this resource. The most specialized scavengers, vultures, mobilize a large part of the nutrients and energy encapsulated in vertebrate carcasses, but many other Accipitridae (primary predators) and members of other families, like Corvidae (omnivores), also scavenge frequently (DeVault et al. 2003; Mateo-Tomás et al. 2015; Olson et al. 2016). Both the multichannel feeding characteristic of facultative scavengers and the typically high number of feeding links involving scavenging (either obligate or facultative) have been identified recently as stabilizing forces in food webs (Wilson and Wolkovich 2011).

The high connectivity of scavenging networks makes it difficult to predict the final outcome of a given perturbation to the food web, with direct bottom-up effects and indirect and complex top-down consequences taking place (Moleón et al. 2014b). Unfortunately, little is known about the ecological consequences of large-scale vulture declines and rarefaction (Ogada et al. 2012a, b), although severe cascading effects can be hypothesized and have indeed likely occurred (see below). Scavenging at the community level is not random but rather is an ordered, nested process in which carcasses visited by poorly specialized scavengers are subsets of those carcasses visited by highly specialized scavengers (Selva and Fortuna 2007). This means that the absence of vultures from the community will trigger strong effects on carrion consumption patterns and the subsequent energy and nutrient flow rates. On one hand, the most obvious effect of the loss of vultures is the decreased rate at which energy and nutrients propagate through food webs (DeVault et al. 2003; Ogada et al. 2012b). On the other hand, less specialized scavengers could potentially then fill this vacant niche and consume more carcasses, which in theory would alter the behavior and demography not only of facultative scavengers themselves, but also of other organisms directly or indirectly connected within the same food web (Moleón et al. 2014b). Processes such as hyperpredation (Courchamp et al. 2000) are therefore prone to emerge following vulture declines. For instance, populations of facultative mammalian scavengers such as feral dogs and rats seem to have increased as a consequence of the recent dramatic vulture population collapse in India, and this could have increased the predation impact of these predators on other wildlife (Pain et al. 2003).

There also might be important ecological consequences when facultative scavengers become locally rare or are extirpated (Olson et al. 2012). The nested nature of carrion consumption patterns predicts that the most specialized scavengers, vultures, are not able to functionally compensate for the extirpation of facultative avian scavengers, as the latter will normally feed on carcasses after the former are satiated. Instead, other vertebrates, invertebrates, and microorganisms are expected to use carrion at higher rates when avian facultative scavengers are absent or scarce. Because most carrion biomass is consumed by vertebrates (DeVault et al. 2003), important indirect effects related to wildlife and human health would likely result from the loss of facultative avian scavengers. Food web changes associated with the extirpation of facultative avian scavengers are expected to be more profound outside vultures' distributional ranges, where facultative scavengers normally visit more carcasses than they do in vulture-dominated environments.

### *Regulating Services*

DISEASE AND PEST CONTROL. Consuming carcasses of wild and domestic animals has been the most enduring ecosystem service provided by scavengers to humans (Moleón et al. 2014a), as reducing the exposure to rotting matter strongly contributes to reducing the rates of transmission of infectious diseases (Ogada et al. 2012b). In the absence of obligate scavengers, facultative scavengers may increase the rate at which they ingest carrion, thus buffering ecosystem functioning to some extent (Şekercioğlu et al. 2004). But as illustrated by the increase in rats and feral dogs following severe population declines of vultures in India, drastic population declines of obligate scavengers could strongly favor some opportunistic facultative scavengers by releasing them from carcass competition (Markandya et al. 2008). Thus, the surplus of carcasses available in the absence of vultures might lead, at least partly, to a population increase wherein opportunistic scavengers could be considered as pests (i.e., as being detrimental to humans or human concerns). The Indian paradigm is a good example of that, and several authors have noted human health risks associated with elevated populations of dogs and rats, the primary reservoirs for rabies and bubonic plague respectively (Pain et al. 2003; Markandya et al. 2008). Moreover, rat and dog bites themselves are a threat to humans (Markandya et al. 2008). Similar problems are expected to emerge in other areas with severe vulture population declines, as in many African regions (Ogada et al. 2012a). In Zimbabwe, for instance, feral dogs dominate carcasses outside protected reserves but not inside them, where vultures are still present and serve as the major scavengers (Butler and du Toit 2002). Therefore, healthy vulture populations may well be key to effective pest control worldwide (Moleón et al. 2014a).

ENVIRONMENTAL AND ECONOMIC COSTS OF SUPPLANTING ECOSYSTEM SERVICES PROVIDED BY SCAVENGERS. In accordance with certain sanitary guidelines, dead livestock has been systematically removed from large regions, as was done in Europe after the bovine spongiform encephalopathy (BSE) crisis (see "Sanitary policies," below). Both government agencies and farmers have been paying for carcass transport and incineration for more than a decade, a service that vultures and other scavengers have provided cost-free for centuries. In Spain alone it is estimated that on average, vultures remove 134 to 201 t of bones and 5,551 to 8,326 t of meat each year, leading to a minimum annual savings of €0.91 to 1.49 million (€0.97–1.60 million throughout the entire European Union; Margalida and Colomer 2012). Later, Morales-Reyes et. al. (2015) estimated that supplanting the natural removal of extensive livestock carrion by scavengers with carcass collection and transport to authorized plants in Spain led to annual emissions of 77,344 metric tons of $CO_2$ eq. to the atmosphere and payments of about $50 million to insurance companies. In another study, Markandya et al. (2008) estimated the human health cost of the vulture decline in India. They calculated the monetary costs (i.e., medicines, doctor remuneration, and work compensation) associated with human rabies transmitted by feral dog bites, which increased dramatically following the Indian vulture crisis, at an estimated US$2.43 billion annually on average. These examples clearly illustrate the important environmental economic and social benefits that vultures can provide to humans.

INDUSTRY SERVICES. Avian scavengers can provide further economic benefits to humans through several traditional industrial activities. In India, for instance, bones from dead cattle are gathered by bone collectors and transported to supply the fertilizer industry. Vultures greatly facilitate bone collection by efficiently cleaning cattle carcasses. In the absence of vultures, the bones would be less readily available, of poorer quality, less hygienic (due to the presence of more rotten flesh), and more difficult to collect (Markandya et al. 2008).

### *Cultural Services*

INTELLECTUAL, SPIRITUAL, AND AESTHETIC INSPIRATION. Modern humans have inherited a strong cultural benefit from the ancient and changing interspecific interactions between closely related *Homo* species and avian and other scavengers since the Plio/Pleistocene transition (Moleón et al. 2014a). Earliest Pliocene archaeological assemblages (2.5 mya) demonstrate that a major function of the earliest known human tools was meat and marrow processing of large carcasses. This human behavior extended well into the Pleistocene (Heinzelin et al. 1999). These early tools may resemble or mimic adaptations of vultures and hyenas for processing of carcasses. They may well have been essential for successful competition with better adapted natural scavengers. Thus, competition with other scavengers probably contributed to the perfection of these human tools and their use, and hence to cultural diversity. Around the same time, selective pressures associated with confrontational scavenging probably triggered perhaps the most distinctive features of *Homo* species: language and collaborative cooperation (Bickerton and Szathmáry 2011). Also, endurance running probably emerged in our lineage as a response to the foraging challenges imposed by the scattered and ephemeral resource that is carrion (Bramble and Lieberman 2011). Ultimately, improved diet quality due to increasing meat consumption, first from active scavenging and then from hunting, has been related, along with other factors, to the extraordinary brain enlargement within the human lineage (Leonard et al. 2007; Bramble and Lieberman 2011; Navarrete et al. 2011).

There are many examples of the spiritual services provided by vultures since approximately 200 kya (Moleón et al. 2014a). Recent studies suggest that Neanderthals widely exploited birds, particularly scavengers, for their feathers and claws as personal ornaments in symbolic behavior (Finlayson et al. 2012). Similarly, many cultures had closed symbolisms and myths involving vultures (Sekercioglu 2006). For example, Egyptians represented the goddess Nebjet as a vulture, and Native Americans from North America to Patagonia included condors as one of their main cultural symbols (Gordillo 2012). Also, the funeral ceremonies of numerous human cultures around the world consisted of offering the corpses of dead relatives to vultures (Donázar 1993; Eaton 2003). All these cultural and spiritual scenarios survive locally today (Moleón et al. 2014a). Humans compete for carrion in some African regions (O'Connell et al. 1988). Zoroastrianism-practicing Parsis and Tibetan Buddhists in Asia maintain the tradition of leaving human corpses to vultures for purification. Certain Native American cultures maintain traditions and festivities linked to condors. Moreover, the presence of vultures and other avian scavengers in artistic, literary, and musical expression is currently widespread (Donázar 1993; Gordillo 2002). The decline of vultures worldwide could lead to the loss of these ancient cultural and spiritual services.

RECREATIONAL SERVICES AND ECOTOURISM. Ecotourism has become a major economic resource and development tool for many regions and countries (Weaver 2008). Recreation and ecotourism activities associated with avian scavengers are flourishing worldwide (Moleón et al. 2014a). There is an increasing interest in viewing and photographing vultures and other carrion eaters such as eagles. Public agencies, nongovernmental organizations, and travel agencies are explicitly advertising and offering these opportunities (Becker et al. 2005; Piper 2005; Markandya et al. 2008; Weaver 2008; Donázar et al. 2009a). Becker et al. (2005) estimated that the potential annual value of viewing threatened griffon vultures (*Gyps fulvus*) at a nature reserve in Israel was from US$1.1 to $1.2 million, and that 85% of the visitors came to the park to view vultures. There are many other examples of the actual and potential value of ecotourism around vulture breeding areas and feeding stations as important engines for local economies (Anderson and Anthony 2005; Piper 2005; Ferrari et al. 2009).

### *Supporting Services*

Avian scavengers consume much of the huge biomass encapsulated in vertebrate carcasses. As seen above, the absence of vultures can retard the rate at which nutrients are redistributed through the ecosystem (DeVault et al. 2003; Ogada et al. 2012b). Thus, avian scavengers play an important role in nutrient cycling.

## Global Challenges to Scavenger Conservation in a Changing World

Populations of obligate scavengers have significantly declined over the last several decades across the globe, mainly due to a suite of anthropogenic factors. Scavengers are the most threatened avian functional group (chapter 12, fig. 6; Şekercioğlu et al. 2004) and 61% of the obligate avian scavengers of the world are currently threatened with extinction (BirdLife International 2014; Ogada et al. 2012a). Many of these species have therefore become high priorities for conservation. This is exemplified by the Egyptian vulture (*Neophron percnopterus*), a formerly widespread and common species, whose decline from least concern to endangered in 2007 was one of the fastest declines in conservation status of any bird species. Specific threats to scavengers vary regionally, but most scavenger species are highly susceptible to anthropogenic disturbances, owing to their unique life history traits. In particular, habitat loss and human persecution have played a prominent role in vulture declines in many regions. However, unintentional poisoning has emerged as one of the greatest threats to avian scavengers globally (Ogada et al. 2012a).

### *Poisoning and Other Environmental Contaminants*

Vultures are particularly vulnerable to contaminants, due to their reliance on carrion. Because they often feed communally, large numbers can be poisoned at a single carcass. In particular, the deliberate poisoning of carnivores by humans is likely the most widespread cause of vulture poisoning worldwide (Donázar 1993; Margalida 2012; Ogada et al. 2012a). The chain of secondary poisoning initiated by the use of poisoned baits ultimately affects vultures and other scavengers. Although the use of poisons to manage carnivore populations has been banned in many countries, it continues to be a common illegal tool used in some regions to manage game species and protect livestock (Hernández and Margalida 2008, 2009a; Ogada et al. 2012a).

Recent links between catastrophic vulture declines and unintentional

FIGURE 8.6. Adult white-backed vulture (*Gyps africanus*) perched near a buffalo carcass in the Hluhluwe-iMfolozi Park, South Africa. Africa holds the richest diversity of vulture species in the planet. Unfortunately, the current threats to African vultures are manifold, with intentional poisoning and food shortage probably being the most widespread. As a result, vultures are increasingly disappearing from large areas and are confined to fewer and fewer secure, protected reserves. Photo by David Carmona.

poisoning through consumption of the veterinary drug diclofenac, a nonsteroidal antiinflammatory drug administered to livestock, has drawn international attention to the vulnerability of scavengers to environmental contamination. In Asia, for example, populations of *Gyps* vultures declined by more than 95% over the last two decades due to accidental poisoning through the consumption of livestock treated with diclofenac (Green et al. 2004; Oaks et al. 2004; Shultz et al. 2004). Vultures consuming livestock with diclofenac-contaminated tissues often die within days from kidney failure (Oaks et al. 2004), but susceptibility to the toxic effects of this drug is not consistent among all avian scavengers (Rattner et al. 2008; Margalida et al. 2014a). Nonetheless, this rapid and widespread crisis has captivated international attention and sparked an unprecedented scientific interest in vultures and other scavengers (Koenig 2006; Margalida et al. 2014a).

Ingestion of pellets or fragments from lead bullets poses another significant threat to some scavengers (Hunt et al. 2006; Kelly et al. 2011; Lambertucci et al. 2011). Upon impact, lead bullets often fragment and become lodged in muscle and soft tissue, where they become available to scavengers that consume viscera or muscle tissue from field-processed and unrecovered big game. Although the use of lead shot was banned for waterfowl hunting in the United States in 1991, lead-based ammunition is still used legally to harvest upland birds and big game throughout most of the United States. Today, lead poisoning remains the leading cause of death for the California condor (*Gymnogyps californianus*), and is perhaps the primary factor threatening the recovery of this species (Cade 2007). Similarly, elevated lead exposure linked to hunting also has been documented for turkey vultures, as well as for a diversity of facultative avian scavengers such as common ravens (*Corvus corax*), great horned owls (*Bubo virginianus*), red-tailed hawks (*Buteo jamaicensis*), golden eagles (*Aquila chrysaetos*), and bald eagles (*Haliaeetus leucocephalus*; Clark and Scheuhammer 2003; Craighead and Bedrosian 2009; Kelly et al. 2011; Kelly and Johnson 2011). In Europe, lead poisoning has been identified in several avian scavengers, such as the Egyptian vulture (Gangoso et al. 2009) and bearded vulture (Hernández and Margalida 2009b).

Although diclofenac and other environmental contaminants that cause rapid mortality have received widespread attention, scavengers are also exposed to numerous other toxicants that may have sublethal effects that often go unnoticed (Kumar et al. 2003). For example, more than 50% of bald eagles admitted to wildlife rehabilitators in Iowa had ingested lead, presumably scavenged from hunter-killed white-tailed deer (*Odocoileus virginianus*) remains left in the field (Neumann 2009). Such sublethal exposure to heavy metals may affect bone mineralization (Gangoso et al. 2009), reduce muscle and fat concentrations (Carpenter et al. 2003), and cause organ damage, internal lesions (Pattee et al. 1981), and reduced hatching success (Steidl et al. 1991).

### *Climate Change*

Scavengers, particularly obligate scavengers, are inextricably linked to the distribution and availability of carrion. Thus, any shift in the quantity or temporal stability of carrion resources profoundly affects the composition and dynamics of scavenging communities. Availability of carrion is highly modulated by climate (DeVault et al. 2004; Selva et al. 2005; Parmenter and MacMahon 2009; DeVault et al. 2011) and trophic integrity (Wilmers et al. 2003a, b; Wilmers and Post 2006). Thus, a critical research priority is to elucidate the impact of anthropogenic perturbations to ecosystems, as well as to environmental contamination, on scavenging communities (Beasley et al. 2015).

Climate change is causing phenological mismatch in plant and animal communities worldwide and already resulting in bird population declines (Wormworth and Şekercioğlu 2011). However, little is known about the effects of climate change on the phenology of carrion and the scavengers that depend on it. Altered temperature and precipitation patterns resulting from climate change may shift the spatial and temporal availability of carrion, thus impacting scavenging communities across the globe (Smith et al. 2008; Wilson and Wolkovich 2011). For example, the incidence and geographic range of many diseases is projected to increase in response to global climate change (Patz et al. 1996; Harvell et al. 2002). Rather than providing a consistent increase in animal mortality, such increases would likely produce pulses of animal death, thus disrupting the temporal availability of carrion within ecosystems. Changes in the temporal and spatial distribution of carrion, mainly its aggregation, significantly reduce the diversity and evenness of carrion consumption among scavengers (Wilmers et al. 2003a; Cortés-Avizanda et al. 2012), potentially reducing the overwinter survival or fecundity of facultative scavengers that rely on carrion through the winter (Fuglei et al. 2003). However, the impact of truncated carrion availability would probably be more severe for obligate scavengers, with widespread implications for their conservation.

Climate change may also alter competitive interactions between vertebrate scavengers and microbes, potentially reducing vertebrate biodiversity in terrestrial ecosystems. Microbial decomposition doubles with every 10 °C increase in temperature (Vass et al. 1992; Parmenter and MacMahon 2009), suggesting that carrion availability to vertebrates could decrease by 20 to 40%, based on current projections of climate change models (Beasley et al. 2012). Given that the majority of obligate scavengers are currently threatened with extinction (fig. 12.1; Ogada et al. 2012a), such reductions in carrion could contribute to further population declines through resource provisioning (see below).

### *Sanitary Policies*

Carcasses of unstabled livestock have been historically left at their death sites, thus producing an unpredictable and dispersed collection of carcasses throughout the landscape (Donázar et al. 1997). These traditional livestock disposition practices have supported many populations of avian scavengers for centuries (Donázar et al. 1997; Tella 2001). However, anthropogenic activities also can put this beneficial and reciprocal coexistence of vultures and humans at risk. This occurred recently in Europe with the detection of variant (vCJD) and new variant (nvCJD) Creutzfeldt-Jakob disease in humans, which was acquired from cattle infected by bovine spongiform encephalopathy (BSE). The subsequent application of restrictive sanitary legislation (Regulation CE 1774/2002) greatly limited the use of animal by-products that were not intended for human consumption. This legislation required that all carcasses of domestic animals had to be collected from farms and processed or destroyed in authorized facilities. As a result of these sanitary regulations, supplementary feeding points for vultures supplied by intensive farming have greatly diminished (80%) throughout Spain since 2006. The dichotomy between sanitary and environmental policies (i.e., eliminating carcasses versus conserving scavenger species) led to several European dispositions that regulated the use of animal by-products as food for scavenging birds (Tella 2001; Donázar et al. 2009a, 2009b; Margalida et al. 2010).

As a consequence of food shortages, several demographic warning signals have been documented in avian scavengers, including halted population growth, decreased breeding success, apparent increased mortality among younger age classes, and increases in the number of aggressive interactions with live livestock (Donázar et al. 2009a; Margalida et al. 2011b; Margalida et al. 2014b). An immediate solution applied by managers and conservationists has been the implementation of artificial feeding sites and vulture restaurants to counteract the presumed food shortages. With predictable food resources, habitat quality has been modified, and the regular use of feeding stations by vultures and other scavengers could change the ecological services directly and indirectly provided by these species (Deygout et al. 2009; Dupont et al. 2011).

### *Power Lines and Wind Farms*

Global demand for energy is increasing worldwide, leading to an increase in the production and development of both traditional and alternative power sources (Northrup and Witenmeyer 2012), some of which may pose a threat to avian scavengers. For example, electrocution from and collisions with power lines and wind farms have been documented for several vulture species (Ledger and Annegarn 1981; Donázar et al. 2002; Margalida et al. 2008), as well as for facultative avian scavengers such as eagles and ravens (Lehman et al. 2010; Guil et al. 2011). Although the demographic data needed to assess the actual risk that electrocution and collision pose to populations are unavailable, some authors consider that power line mortality is not high enough to affect long-term population size (Bevanger 1994; 1998). Others, however, have identified electrocution as a primary cause of some vulture population declines. For example, Ledger and Annegarn (1980) and Krüger et al. (2004) show that in South Africa the Cape griffon is electrocuted more than any other raptor species. Nikolaus (1984, 2006) and Angelov et al. (2012) advised that electrocutions were responsible for Egyptian vulture declines near Khartoum, Sudan. Leshem (1985) suggested that griffon vulture declines in Israel may result from electrocution and other human-caused factors.

Wind farms have received public and governmental support as alternative energy sources that do not contribute to air pollution, unlike sources associated with fossil fuel technologies (Leddy et al. 1999). During the last decade, wind farm developments have increased substantially all over the world, with the greatest increases occurring in Europe and the United States. The great success achieved by countries such as Germany and Spain in developing the wind power industry serves as an example for all countries interested in expanding wind energy production (Kenisarin et al. 2006). However, the expansion of wind farms has environmental impact (i.e., habitat removal, construction of roads and power lines, visual impact; Laiolo and Tella 2006; Kuvlesky et al. 2007) that must be evaluated and considered. Most research on the subject investigates how wind farm development impacts bird and bat populations (e.g., Langston and Pullan 2003; Baerwald et al. 2008; Garvin et al. 2011). Among all species studied, vultures are among the species most frequently killed by turbines (Carrete et al. 2012). Indeed, in some areas hundreds of individuals have been killed through collisions with turbines, leading to a stoppage of the wind farms' activity in a few cases (Carrete et al. 2010). Moreover, it has been shown that slight increases in mortality at wind farms can significantly affect population trends, thus accelerating the population extinction of sensitive or endangered species (Carrete et al. 2009).

## The Future of Avian Scavenger Conservation

The sustainability of free-ranging populations of many obligate scavenging birds will undoubtedly be dependent upon our ability to recognize and mitigate existing and future threats. While management strategies developed to address the effects of climate change and trophic downgrading remain challenging, the top priorities should be reduction of exposure to harmful veterinary drugs and other toxicants, sanitary regulations consistent with wildlife conservation needs, and reduced habitat alteration (Balmford 2013).

### *Eliminating Intentional Poisoning*

Eliminating deliberate wildlife poisoning is a complex task that must involve legal, educational, economic, and punitive measures. An important advancement in fighting against illegal poisoning is the recent Life Biodiversity project, “Innovative actions against illegal poisoning in EU Mediterranean pilot areas” (http://www.lifeagainstpoison.org). This project joins several conservation and research institutions from three European countries (Portugal, Spain, and Greece) to find practical solutions to the problem that illegal poisoning poses for many threatened species, mostly vultures. Through close cooperation with local governments, hunters, and stockbreeders, this project aims to improve the conservation status of different species by identifying high-risk areas for poisoning, thus raising awareness about the detrimental effects of poisoning and decreasing the sense of impunity among offenders. One of the most innovative and successful actions is the use of trained dogs to find poisoned baits that would otherwise go unnoticed.

### *Sanitary and Veterinary Regulations*

In response to the catastrophic population collapse of avian scavengers in Asia, veterinary use of diclofenac in domesticated livestock was banned in India, Pakistan, and Nepal in 2006. The banning of this drug reduced population declines of several vulture species, including that of the oriental white-backed vulture (*Gyps bengalensis*), which may have even increased slightly in recent years (Balmford 2013). However, additional efforts are needed to completely eliminate diclofenac from carcasses, as the presence of diclofenac in less than 1% of carcasses is sufficient to cause severe population declines in susceptible vultures (Cuthbert et al. 2011). Recent trials evaluating the effects of an alternative nonsteroidal antiinflammatory drug, meloxicam, failed to detect any lethal or sublethal effects on captive or wild *Gyps* vultures (Swan et al. 2006; Swarup et al. 2007). Meloxicam is also of low toxicity to other birds and appears to be rapidly metabolized; this suggests that repeated long-term exposure is unlikely to negatively impact scavengers (Swarup et al. 2007). However, additional trials evaluating the impact of meloxicam and other veterinary drugs on scavengers, as well as reduced presence of diclofenac in livestock carcasses, are needed to ensure the recovery of critically endangered *Gyps* vultures. Veterinary treatments should also be carefully applied to both stabled and unstabled livestock to reduce the prevalence of other antiinflammatory, antibiotic, and antiparasitic agents (Donázar et al. 2009a).

Legislation to minimize wildlife exposure to lead also should be implemented or improved, depending on the country, to reduce the effects of lead on large predatory and scavenging birds, including emblematic species such as the California condor. For this reason, lead ammunition was banned from use for big-game hunting within portions of the condor's range in 2008. After this ban, blood lead concentrations decreased 2.5 to 3 times in both golden eagles and turkey vultures, suggesting that a complete ban of lead ammunition would decrease lead exposure for many scavengers (Kelly et al. 2011).

The BSE crisis in Europe required new sanitary regulations for both human health and ecological reality. Fortunately, recommendations made by scientists, conservationists, and managers have recently led to new European guidelines allowing farmers to abandon dead animals in the field and/or feeding stations (Margalida et al. 2012). This illustrates how scientific arguments can trigger positive political action and help to reconcile conservation challenges and human activities (Sutherland et al. 2004; Margalida et al. 2012).

### *Improving Power Lines and Wind Farms*

Measures to mitigate electrocution and collisions include reviewing the placement of new electric lines, removing earth wires or fitting them with markers, and changing pylon design. Such measures have been used in several countries, particularly in Europe, North America, and South Africa (Lehman et al. 2007). For example, low-utility and medium-voltage distribution lines have been placed underground in the Netherlands, Belgium, the United Kingdom, Norway, Denmark, and Germany. Also, most countries in southern Europe require all poles and technical components of power lines to be manufactured and constructed in a way that is safe for birds and protects them from electrocution (Schürenberg et al. 2010). In Spain, several efforts have identified mortality hotspots and modified pylons and lines (Tintó et al 2010). In South Africa, the collision rates of some species such as cranes and bustards were partially reduced after bird-flight diverters were attached to ground wires (Anderson 2002). Regrettably, the actual effectiveness of these measures for vultures is unknown, although for other raptor species some mortality reductions have been reported (Benson 1981).

In the case of wind-farm mortality, our understanding of the problem is less advanced, and mitigation often fails (Drewitt and Langston 2006). Hence the most effective guideline for wind farms is to place them far from sensitive species (Carrete et al. 2012). Recent research found that vultures possess large visual fields that provide comprehensive coverage of the ground ahead and the sky on either side, but which leave large blind spots above and below their heads. Thus, when vultures fly, they tilt their heads downwards so that the space directly in front of them becomes a blind area (Martin et al. 2012).

Demographic studies indicate that fecundity and survival of vultures are negatively influenced by mortality at wind turbines (Carrete et al. 2009; Martínez-Abraín et al. 2011; no data available for power lines), and that small reductions in the survival of territorial and nonterritorial birds associated with wind farms can strongly impact the population viability of these long-lived species (Carrete et al. 2009). Altogether, existing data highlight the need to examine the long-term impact of power lines and wind farms rather than focusing on short-term mortality, as is often promoted by power companies and some wildlife agencies. Unlike other non-natural causes of mortality which are difficult to eradicate or control, power line and wind farm fatalities can be lowered by powering down or removing risky poles (or entire lines) or turbines (or entire farms) and, in certain cases, by placing them outside areas critical for endangered birds.

### *Vulture Restaurants*

Some countries have created feeding stations where carcass piles are maintained to provide supplemental food to threatened or at-risk avian scavengers. Vulture restaurants, vulture feeding stations, or *muladares* were first created in the late 1960s in both the French and the Spanish slopes of the Pyrenees (Donázar 1993). The impetus was the unfounded but pervasive idea that food shortage resulting from the progressive transformation of traditional systems of animal husbandry was a major cause of the widespread decline of vultures in Europe. Since that time, vulture feeding stations have played an essential role in many avian scavenger conservation programs worldwide, including reintroductions, recoveries of small populations, and range expansions (Donázar et al. 2009a). Several advantages have been traditionally attributed to vulture restaurants (see reviews in Anderson and Anthony 2005; Piper 2005; Donázar et al. 2009a). The most obvious benefit is the provision of food in situations of presumed temporal or, above all, spatial food scarcity (Moreno-Opo et al. 2015a). Vulture restaurants are also generally safe places for birds to feed; they provide poison-free food, keep avian scavengers out of poisoning areas (Oro et al. 2008), and supplement vulture diets with rare nutrients like calcium. As indirect benefits, vulture restaurants can be important for raising awareness among landowners, farmers, and the general public, and for ecotourism and science (e.g., as places for scientists to read the bands or wing tags of marked birds).

Despite these benefits, vulture restaurants should not be conceived as the panacea for vulture conservation in modern times. Numerous objections to these artificial feeding schemes have been identified or suggested (Anderson and Anthony 2005; Piper 2005; Donázar et al. 2009a). First and most important, it remains unclear whether food provisioning improves the long-term viability of the target populations, although some local population recoveries have been partially attributed to such programs (Donázar et al. 2009a). Benefits to some demographic parameters, such as an increase in pre-adult survival (Oro et al. 2008), can be counteracted by density-dependent processes (Carrete et al. 2006a) and behavioral changes (Carrete et al. 2006b) that compromise the long-term success of these management actions (Donázar et al. 2009a). Second, vulture restaurants are single places in which food is supplied at a fairly constant rate. This differs from the ecological context in which vultures evolved, with food available only randomly in space and time and located by searching strategies based on long-distance movements and using behavioral processes such as social facilitation and information sharing (Cortés-Avizanda et al. 2012; Kane et al. 2014). The repercussions of this scenario on individuals, populations, and communities of avian scavengers are largely unknown, but are undoubtedly significant (Donázar et al. 2009a). The accumulation of carrion in a single place favors the most numerous and dominant species in the guild, so that other species, which often are more threatened, are nonetheless excluded from this conservation-motivated food source (Cortés-Avizanda et al. 2010, 2012; Moreno-Opo et al. 2015b).

### *Societal Involvement and Ecotourism*

Societal involvement is essential in any modern conservation strategy. Any initiative aimed at spreading awareness of the ecological value of avian scavengers should be welcomed, especially in educational and academic arenas. Interdisciplinary and international cooperation is also highly desirable for global awareness about avian scavengers. A good example of this is the annual International Vulture Awareness Day (September 1; www.vultureday.org), which was established recently as a way to bring the public closer to the problems affecting vultures and the actions of scientists and conservationists to address them. This initiative, consisting of internationally coordinated and media-covered activities including talks and censuses, resulted from cooperation by the South African Endangered Wildlife Trust (Birds of Prey Programme) and the English Hawk Conservancy Trust. It is now joined by both public and private conservation organizations, as well as by many other people around the world who are concerned with vultures.

The growing source of income associated with vulture and eagle viewing and photography is emerging as a powerful conservation tool, provided that part of the profits are allocated to endangered avian scavenger management programs and also to the benefit of local human communities (Becker et al. 2005; Piper 2005; Donázar et al. 2009a). However, further research is needed to widely evaluate the current economic value and future potential of avian scavenger tourism (Becker et al. 2005). Care should be taken that human presence does not induce potential selective pressures on those wild populations (Carrete and Tella 2010).

## Ecosystem Disservices

Vultures are resistant to bacterial toxins in decomposing carcasses (Houston and Cooper 1975), and they decrease the propagation of some diseases. Ogada et al. (2012b) showed that, in the absence of vultures, the time necessary for complete depletion of carcasses nearly tripled, and that the number of carnivorous mammals (which are known to spread some diseases) using carcasses increased threefold. Also, the collapse of vulture populations in Asia apparently led to increases in the number of feral dogs and rats (Pain et al. 2003), coinciding with substantial increases in the prevalence of human rabies (Markandya et al. 2008). Thus, vultures and other avian scavengers play an important role in limiting disease spread overall. Even so, some research suggests that in certain circumstances, scavengers might propagate disease (see Jennelle et al. 2009). For example, VerCauteren et al. (2012) demonstrated that infectious scrapie prions survived passage through the digestive systems of American crows (*Corvus brachyrhynchos*), and speculated that the crows could proliferate


FIGURE 8.7. The black vulture (*Coragyps atratus*) is a species of New World vulture whose range extends from the Midwestern United States to central Chile. This individual has been marked with a uniquely numbered patagial tag to allow researchers to collect data on the population dynamics and behavior of the species. Photo by James C. Beasley.

prion diseases. However, relatively little is known about how avian scavengers influence disease ecology. Additional research in this area would be beneficial to humans and wildlife (fig. 8.7).

## Acknowledgments

We thank our respective institutions for funding support during the preparation of this chapter, and Elizabeth Poggiali for assistance in proofing and formatting. This work was partially funded by project CGL2012-40013-C02-02 Spanish Government. Bradley F. Blackwell, Thomas W. Seamans, and Mark E. Tobin provided helpful comments on the manuscript. The input of James C. Beasley was supported through funding provided by the US Department of Energy under Award Number DE-FC09-07SR22506 to the University of Georgia Research Foundation. This work has partially been funded by the Spanish Ministry of Economy and Competitiveness through grant no. CGL2012-40013-C02-01/02 MIMECO and FEDER funds.

## References

Álvarez, F., de Reyna, A., and Hiraldo, F. 1976. Interactions among avian scavengers in southern Spain. *Ornis Scandinavica* 2:215–26.

Anderson, M. D. 2002. Karoo large terrestrial bird powerline project, report no. 1. Johannesburg: Eskom (unpublished report).

Anderson, M. D., and Anthony, A. 2005. The advantages and disadvantages of vulture restaurants versus simply leaving livestock (and game) carcasses in the veldt. *Vulture News* 53:42–45.

Balmford, A. 2013. Pollution, politics, and vultures. *Science* 339:653–54.

Barton, P. S., Cunningham, S. A., Lindenmayer, D. B., and Manning, A. D. 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia* 171:761–72.

Beasley, J. C., Olson, Z. H., and DeVault, T. L. 2012. Carrion cycling in food webs: Comparisons among terrestrial and marine ecosystems. *Oikos* 121:1021–26.

Beasley, J. C., Olson, Z. H., and DeVault, T. L., 2015. Ecological role of vertebrate scavengers. In *Carrion Ecology, Evolution and Their Applications*, E. M. Benhow, J. Tomberlin, and A. Tarone, eds., 107–27. CRC Press, Boca Raton, FL.

Becker, N., Inbar, M., Bahat, O., Choresh, Y., Ben-Noon, G., and Yaffe, O. 2005. Estimating the economic value of viewing griffon vultures *Gyps fulvus*: A travel cost model study at Gamla Nature Reserve, Israel. *Oryx* 39:429–34.

Ben-David, M., Hanley, T. A., Klein, D. R., and Schell, D. M. 1997. Seasonal changes in diets of coastal and riverine mink: The role of spawning Pacific salmon. *Canadian Journal of Zoology* 75:803–11.

Bevanger, K. 1994. Bird interactions with utility structures: Collision and electrocution, causes and mitigation measures. *Ibis* 136:412–25.

———. 1998. Biological and conservation aspects of bird mortality caused by electricity power lines: A review. *Biological Conservation* 86:67–76.

Bickerton, D., and Szathmáry, E. 2011. Confrontational scavenging as a possible source for language and cooperation. *BMC Evolutionary Biology* 11:261.

BirdLife International. 2014. IUCN Red List for Birds. Accessed September 5, 2014. http://www.birdlife.org.

Blanchard, B. M., and Knight, R. R. 1990. Reactions of grizzly bears, *Ursus arctos horribilis*, to wildfire in Yellowstone National Park, Wyoming. *Canadian Field-Naturalist* 104:592–94.

Bramble, D. M., and Lieberman, D. E. 2011. Endurance running and the evolution of *Homo*. *Nature* 432:345–52.

Buechley, E. R., Şekercioğlu, Ç. H. 2016a. The avian scavenger crisis: Looming extinctions, trophic cascades, and loss of critical ecosystem function. *Biological Conservation*. In press.

Buechley, E. R., Şekercioğlu, Ç. H. 2016b. Vanishing vultures: The collapse of critical scavengers. *Current Biology*. In press.

Bump, J. K., Peterson, R. O, and Vucetich, J.A. 2009. Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. *Ecology* 90:3159–67.

Burkepile, D. E., Parker, J. D., Woodson, C. B., Mills, H. J., Kubanek, J., Sobecky, P. A., and Hay, M. E. 2006. Chemically mediated competition between microbes and animals: Microbes as consumers in food webs. *Ecology* 87:2821–31.

Butler, J. R. A., and du Toit, J. T. 2002. Diet of free-ranging domestic dogs (*Canis familiaris*) in rural Zimbabwue: Implications for wild scavengers on the periphery of wildlife reserves. *Animal Conservation* 5:29–37.

Cade, T. J. 2007. Exposure of California condors to lead from spent ammunition. *Journal of Wildlife Management* 71:2125–33.

Carpenter, J. W., Pattee, O. H, Fritts, S. H, Rattner, B. A., Wiemeyer, S. N., Royle, J. A., and Smith, M. R. 2003. Experimental lead poisoning in turkey vultures (*Cathartes aura*). *Journal of Wildlife Diseases* 39:96–104.

Carrete, M., Donázar, J. A., and Margalida, A. 2006a. Density-dependent productivity depression in Pyrenean bearded vultures: Implications for conservation. *Ecological Applications* 16:1674–82.

———. 2006b. Linking ecology, behaviour and conservation: Does habitat saturation change the mating system of bearded vultures? *Biology Letters* 2: 624–27.

Carrete, M., Sánchez-Zapata, J. A, Benítez, J. R, Lobón, M., and Donázar, J. A. 2009. Large scale risk-assessment of wind-farms on population viability of a globally endangered long-lived raptor. *Biological Conservation* 142:2954–61.

Carrete, M., Sánchez-Zapata, J. A, Benítez, J. R., Lobón, M., Montoya, F., and Donázar, J. A. 2012. Mortality at wind-farms is positively correlated to large-scale distribution and aggregation in griffon vultures. *Biological Conservation* 145:102–8.

Carrete, M., and Tella, J. L. 2010. Individual consistency in flight initiation distances in burrowing owls: A new hypothesis on disturbance-induced habitat selection. *Biology Letters* 6:167–70.

Chaudhry, M., Arshad, S., Ali Mahmood, A., and Khan, A. A. 2004. Diclofenac residues as the cause of vulture population decline in Pakistan. *Nature* 427: 630–33.

Clark, A. J., and Scheuhammer, A. M. 2003. Lead poisoning in upland-foraging birds of prey in Canada. *Ecotoxicology* 12:23–30.

Cooper, S. M., Holekamp, K. E., and Smale, L. 1999. A seasonal feast: Long-term analysis of feeding behaviour in the spotted hyaena (*Crocuta crocuta*). *African Journal of Ecology* 37:149–60.

Cortés-Avizanda, A., Carrete, M., and Donázar, J. A. 2010. Managing supplementary feeding for avian scavengers: Guidelines for optimal design using ecological criteria. *Biological Conservation* 143:1707–15.

Cortés-Avizanda, A., Jovani, R., Carrete, M., and Donázar, J. A. 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: A field experiment. *Ecology* 93:2570–79.

Courchamp, F., Langlais, M., and Sugihara, G. 2000. Rabbits killing birds: Modelling the hyperpredation process. *Journal of Animal Ecology* 69:154–64.

Craighead, D. and Bedrosian, B. 2009. A relationship between blood lead levels of common ravens and the hunting season in the southern Yellowstone Ecosystem. In *Ingestion of Lead from Spent Ammunition: Implications for Wildlife and Humans*, ed. R. T. Watson, M. Fuller, M. Pokras, and W. G. Hunt. Boise, ID: Peregrine Fund.

Cuthbert, R., Taggart, M. A., Prakash, V., Saini, M., Swarup, D., Upreti, S., Mateo, R., Sunder Chakraborty, S., Deori, P., and Green, R. E. 2011. Effectiveness of action in India to reduce exposure of *Gyps* vultures to the toxic veterinary drug diclofenac. *PLoS ONE* 6(5):e19069.

Danell, K., Berteaux, D., and Brathen, K. A. 2002. Effect of Muskox Carcasses on Nitrogen Concentration in Tundra Vegetation. *Arctic* 55:389–92.

DeVault, T. L., Brisbin, I. L. Jr., and Rhodes, O. E. Jr. 2004. Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. *Canadian Journal of Zoology* 82:502–9.

DeVault, T. L., and Krochmal, A. R. 2002. Scavenging by snakes: An examination of the literature. *Herpetologica* 58:429–36.

DeVault, T. L., Olson, Z. H., Beasley, J. C., and Rhodes, O. E. Jr. 2011. Mesopredators dominate competition for carrion in an agricultural landscape. *Basic and Applied Ecology* 12:268–74.

DeVault, T. L., Rhodes, O. E. Jr., and Shivik, J. A. 2003. Scavenging by vertebrates: Behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102:225–34.

Donázar, J. A. 1993. *Los buitres ibéricos*. Madrid: Ed. Quercus.

Donázar, J. A., Margalida, A., and Campión, D., eds. 2009a. *Vultures, Feeding Stations and Sanitary Legislation: A Conflict and Its Consequences from the Perspective of Conservation Biology*. Spain: Sociedad de Ciencias Aranzadi.

Donázar, J. A., Margalida, A., Carrete, M., and Sánchez-Zapata, J. A. 2009b. Too sanitary for vultures. *Science* 326:664.

Donázar, J. A., Naveso, M. A., Tella, J. L., and Campión, D. 1997. Extensive grazing and raptors in Spain. In *Farming and Birds in Europe*, ed. D. Pain and M. W. Pienkowsky, 117–49. London: Academic Press.

Drewitt, A. L., and Langston, R. H. W. 2006. Assessing the impacts of wind farms on birds. *Ibis* 148:29–42.

Dudley, J. P. 1996. Record of carnivory, scavenging and predation for *Hippopotamus amphibius* in Hwange National Park, Zimbabwe. *Mammalia* 60:486–88.

Dunne, J. A., Williams, R. J., and Martinez, N. D. 2002. Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecology Letters* 5:558–67.

Dupont, H., Mihoub, J.-B., Bobbe, S., and Sarrazin, F. 2012. Modelling carcass disposal practices: Implications for the management of an ecological service provided by vultures. *Journal of Applied Ecology* 49:404–11.

Duriez, O., Herman, S., and Sarrazin, F. 2012. Intra-specific competition in foraging Griffon Vultures *Gyps Fulvus*: 2. The influence of supplementary feeding management. *Bird Study* 59:193–206.

Eaton, J. 2003. Silent towers, empty skies. *Earth Island Journal* 18(4): 30–33.

Errington, P., and Breckenridge, W. 1938. Food habits of buteo hawks in north-central United States. *Wilson Bulletin* 50:113–21.

Ferrari, S., MacNamara, M., Albrieu, C., Asueta, R., and Alarcón, S. 2009. The use of wild fauna for the promotion of ecotourism activities: The case of the Andean condor (*Vultur gryphus*) in the Río Turbio coal basin. *Ambientalmente Sustentable* 8:173–84.

Finlayson, C., Brown, K., Blasco, R., Rosell, J., Negro, J. J., et al. 2012. Birds of a feather: Neanderthal exploitation of raptors and corvids. *PLoS ONE* 7:e45927.

Fuglei, E., Oritsland, N. A., and Prestrud, P. 2003. Local variation in arctic fox abundance on Svalbard, Norway. *Polar Biology* 26:93–98.

Gangoso, L., Agudo, R., Anadón, J. D., de la Riva, M., Suleyman, A. S., Porter, R., and Donázar, J. A. 2013. Reinventing mutualism between humans and wild fauna: Insight from cultures as ecosystem services providers. *Conservation Letters* 6:172–79.

Gangoso, L., Álvarez-Lloret, P., Rodríguez-Navarro, A. A. B., Mateo, R., Hiraldo, F., and Donázar, J. A. 2009. Long–term effects of lead poisoning on bone mineralization in vultures exposed to ammunition sources. *Environmental Pollution* 157:569–74.

Gennard, D. 2007. *Forensic Entomology: An Introduction*. West Sussex, UK: John Wiley & Sons.

Gibbs, J. P., and Stanton, E. J. 2001. Habitat fragmentation and arthropod community change: Carrion beetles, phoretic mites, and flies. *Ecological Applications* 11: 79–85.

Gordillo, S. 2002. El cóndor andino como patrimonio natural y cultural de Sudamérica. . Córdoba, Argentina: Cuadernos de Taller, 5.

Green, G. I., Mattson, D. J., and Peek, J. M. 1997. Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. *Journal of Wildlife Management* 61:1040–55.

Green, R. E., Taggart, M. A., Das, D., Pain, D. J., Kumar, C. S., Cunningham, A. A., and Cuthbert, R. 2004. Collapse of Asian vulture populations: Risk of mortality from residues of the veterinary drug diclofenac in carcasses of treated cattle. *Journal of Applied Ecology* 43:949–56.

Guil, F., Fernández-Olalla, M., Moreno-Opo, R., Mosqueda, I., García, M. E., Aranda, A., Arredondo, A., Guzmán, J., Oria, J., González, L. M., and Margalida, A. 2011. Minimising mortality in endangered raptors due to power lines: The importance of spatial aggregation to optimize the application of mitigation measures. *PLoS ONE* 6:e28212.

Hairston, N. G., Smith, F. E., and Slobodkin, L. B. 1960. Community structure, population control, and competition. *American Naturalist* 94:421–25.

Hanski, I. 1987. Carrion fly community dynamics: Patchiness, seasonality and coexistence. *Ecological Entomology* 12:257–66.

Hanski, I., and Kuusela, S. 1980. The structure of carrion fly communities: Differences in breeding seasons. *Annales Zoologici Fennici* 17:185–90.

Harvell, C. D., Mitchell, C. E., Ward, J. R., Altizer, S., Dobson, A. P., Ostfeld, R. S., and Samuel, M. D. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296:2158–62.

Heinzelin, J. D., Desmond Clark, J., White, T., Hart, W., Renne, P., WoldeGabriel, G., Beyene, Y., and Vrba, E. 1999. Environment and behaviour of 2.5-Million-Year-Old Buri Hominids. *Science* 284:625–29.

Hernández, M., and Margalida, A. 2008. Pesticide abuse in Europe: Effects on the Cinereous vulture (*Aegypius monachus*) population in Spain. *Ecotoxicology* 17:264–72.

———. 2009a. Poison-related mortality effects in the endangered Egyptian vulture (*Neophron percnopterus*) population in Spain. *European Journal of Wildlife Research* 55:415–23.

———. 2009b. Assessing the risk of lead exposure for the conservation of the endangered Pyrenean bearded vulture (*Gypaetus barbatus*) population. *Environmental Research* 109:837–42.

Hewson, R. 1984. Scavenging and predation upon sheep and lambs in west Scotland. *Journal of Applied Ecology* 21:843–68.

Houston, D. C. 1979. The adaptations of scavengers. In *Serengeti, Dynamics of an Ecosystem*, ed. A. R. E. Sinclair and M. Norton-Griffiths. Chicago: University of Chicago Press.

Houston, D. C., and Cooper, J. 1975. The digestive tract of the whiteback griffon vulture and its role in disease transmission among wild ungulates. *Journal of Wildlife Diseases* 11:306–13.

Hunt, W. G., Burnham, W., Parish, C. N., Burnham, K. K., Mutch, B., and Oaks, J. L. 2006. Bullet fragments in deer remains: Implications for lead exposure in avian scavengers. *Wildlife Society Bulletin* 34:167–70.

Janzen, D. 1977. Why fruits rot, seeds mold, and meat spoils. *American Naturalist* 111:691–713.

Jennelle, C., Samuel, M. D., Nolden, C. A., and Berkley, E. A. 2009. Deer carcass decomposition and potential scavenger exposure to chronic wasting disease. *Journal of Wildlife Management* 73:655–62.

Jinová, B., Podskalská, H., Růzicka, J., and Hoskovec, M. 2009. Irresistible bouquet of death: How are burying beetles (Coleoptera: Silphidae: Nicrophorus) attracted by carcasses. *Naturwissenschaften* 96:889–99.

Johnson, M. D. 1975. Seasonal and microseral variations in the insect populations on carrion. *American Midland Naturalist* 93:79–90.

Kane, A., Jackson, A. L., Ogada, D. L., Monadjem, A., and McNally, L. 2014. Vultures acquire information on carcass location from scavenging eagles. *Proc. R. Soc. B.* 281:20141072.

Kapfer, J., Gammon, D., and Groves, J. 2011. Carrion–feeding by barred owls (Strixvaria). *Wilson Journal of Ornithology* 123:646–49.

Kelly, T. R., Bloom, P. H., Torres, S. G., Hernandez, Y. Z., Poppenga, R. H., Boyce, W. M., and Johnson, C. K. 2011. Impact of the California lead ammunition ban on reducing lead exposure in golden eagles and turkey vultures. *PLoS ONE* 6: e17656.

Kelly, T. R., and Johnson, C. K. 2011. Lead exposure in free-flying turkey vultures is associated with big game hunting in California. *PLoS ONE* 6:e15350.

Kenisarina, M., V. M. Karsli, and M. Caglar. 2006. Wind power engineering in the world and perspectives of its development in Turkey. *Renewable and Sustainable Energy Reviews* 10:341–69.

Koenig, R. 2006. Vulture research soars as the scavengers' numbers decline. *Science* 312:1591–92.

Krofel, M., Kos, I., and Jerina, K. 2012. The noble cats and the big bad scavengers: Effects of dominant scavengers on solitary predators. *Behavioral Ecology and Sociobiology* 66:1297–1304.

Krüger, R., Maritz, A., van Rooyen, C. 2004. Vulture electrocutions on vertically configured medium voltage structures in the Northern Cape Province, South Africa. In Chancellor, R. D., and Meyburg, B.–U. (Eds.), *Raptors Worldwide*. World Working Group on Birds of Prey and Owls, Berlin, Germany, and MME/BirdLife Hungary, Budepest, 437–41.

Kumar, K. S., Bowerman, W. W., DeVault, T. L., Takasuga, T., Rhodes, O. E. Jr., Brisbin, I. L. Jr., and Masunaga, S. 2003. Chlorinated hydrocarbon contaminants in blood of black and turkey vultures from Savannah River Site, South Carolina, USA. *Chemosphere* 53:173–82.

Laiolo, P., and Tella, J. L. 2006. Fate of unproductive and unattractive habitats: Recent changes in Iberian steppes and their effects on endangered avifauna. *Environmental Conservation* 33:223–32.

Lambertucci, S. A., Donázar, J. A., Delgado, A., Jiménez, B., Sáez, M., Sánchez-Zapata, J. A., and Hiraldo, F. 2011. Widening the problem of lead poisoning to a South-American top scavenger: Lead concentrations in feathers of wild Andean condors. *Biological Conservation* 144:1464–71.

Lambertucci, S. A., Trejo, A., Di Martino, S., Sánchez-Zapata, J. A., Donázar, J. A., and Hiraldo, F. 2009. Spatial and temporal patterns in the diet of the Andean condor: Ecological replacement of native fauna by exotic species. *Animal Conservation* 12:338–45.

Ledger, J. A., and Annegarn, H. J. 1981. Electrocution hazards to the cape vulture *Gyps coprotheres* in South Africa. *Biological Conservation* 20:15–24.

Lehman, R. N., Savidge, J. A., Kennedy, P. L., and Harness, R. E. 2012. Raptor electrocution rates for a utility in the intermountain Western United States. *Journal of Wildlife Management* 74:459–70.

Leonard, W. R., Snodgrass, J. J., and Robertson, M. L. 2007. Effects of brain evolution on human nutrition and metabolism. *Annual Review of Nutrition* 27: 311–27.

Leshem, Y. 1985. Griffon Vultures in Israel: Electrocution and other reasons for a declining population. *Vulture News* 13:14–20.

McFarland, W. N., Pough, F. H., Cade, T. J., and Heiser, J. B. 1979. *Vertebrate Life*. New York: Macmillan.

Margalida, A. 2008a. Bearded vultures (*Gypaetus barbatus*) prefer fatty bones. *Behavioural Ecology and Sociobiology* 63:187–93.

———. 2008b. Presence of bone remains in the ossuaries of bearded vultures *Gypaetus barbatus*: Storage or nutritive rejection? *Auk* 125:560–64.

——. 2012. Baits, budget cuts: A deadly mix. *Science* 338:192.

Margalida, A., Bogliani, G., Bowden, C., Donázar, J. A., Genero, F., Gilbert, M., Karesh, W., Kock, R., Lubroth, J., Manteca, X., Naidoo, V., Neimanis, A., Sánchez-Zapata, J. A., Taggart, M., Vaarten, J., Yon, L., Kuiken, T., and Green, R. E. 2014. One health approach to use of pharmaceuticals. *Science* 346:1296–98.

Margalida, A., Campión, D., and Donázar, J. A. 2011b. European vultures' altered behaviour. *Nature* 480:457.

Margalida, A., Carrete, M., Sánchez-Zapata, J. A., and Donázar, J. A. 2012. Good news for European vultures. *Science* 335:284.

Margalida, A., and Colomer, M. A. 2012. Modelling the effects of sanitary policies on European vulture conservation. *Scientific Reports* 2:753.

Margalida, A., Colomer, M. A., and Sanuy, D. 2011a. Can wild ungulate carcasses provide enough biomass to maintain avian scavenger populations? An empirical assessment using a bio-inspired computational model. *PLoS ONE* 6: e20248.

Margalida, A., Donázar, J. A., Carrete, M., and Sánchez-Zapata, J. A. 2010. Sanitary versus environmental policies: Fitting together two pieces of the puzzle of European vulture conservation. *Journal of Applied Ecology* 47:931–35.

Margalida, A., Heredia, R., Razin, M., and Hernández, M. 2008. Sources of variation in mortality of the bearded vulture *Gypaetus barbatus* in Europe. *Bird Conservation International* 18:1–10.

Markandya, A., Taylor, T., Longo, A., Murty, M. N., Murty, S., and Dhavala, K. 2008. Counting the cost of vulture decline: An appraisal of the human health and other benefits of vultures in India. *Ecological Economics* 67:194–204.

Mateo-Tomás, P., Olea, P., Moleón, M., Vicente, J., Botella, F., Selva, N., Viñuela, J., and Sánchez-Zapata, J. A. 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. *Diversity and Distributions* 21:913–24.

Matuszewski, S., Bajerlein, D., Konwerski, S., and Szpila, K. 2011. Insect succession and carrion decomposition in selected forests of Central Europe. Part 3: Succession of carrion fauna. *Forensic Science International* 207:150–63.

McCann, K. 2000. The diversity-stability debate. *Nature* 405:228–33.

McCann, K., Hastings, A., and Huxel, G. R. 1998. Weak trophic interactions and the balance of nature. *Nature* 395:794–98.

Melis, C., Selva, N., Teurlings, L., Skarpe, C., Linnell, J. D. C., and Andersen, R. 2007. Soil and vegetation nutrient response to bison carcasses in Białowieża Primeval Forest, Poland. *Ecological Research* 22:807–13.

Moleón, M., and Sánchez-Zapata, J. A. 2015. The living dead: Time to integrate scavenging into ecological teaching. *BioScience* 65:1003–10.

Moleón, M., Sánchez-Zapata, J. A., Margalida, A., Carrete, M., Donázar, J. A., and Owen-Smith, N. 2014a. Humans and scavengers: The evolution of interactions and ecosystem services. *BioScience* 64: 394–403.

Moleón, M., Sánchez-Zapata, J. A., Sebastián-González, E., and Owen-Smith, N. 2015. Carcass size shapes the structure and functioning of an African scavenging assemblage. *Oikos* 124:1391–1403.

Moleón, M., Sánchez-Zapata, J. A., Selva, N., Donázar, J. A., and Owen-Smith, N. 2014b. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews* 89:1042–1054, doi: 10.1111/brv.12097.

Morales-Reyes, Z., Pérez-Garcia, J. M., Moleón, M., Botella, F., Carrete, M., Lazcano, C., Moreno-Opo, R., Margalida, A., Donázar, J. A., and Sánchez-Zapata, J. A. 2015. Supplanting ecosystem services provided by scavengers raises greenhouse gas emissions. *Scientific Reports* 5:7811.

Moreno-Opo, R., A. Trujillano, and A. Margalida. 2015a. Optimization of supplementary feeding programs for European vultures depends on environmental and management factors. *Ecosphere* 6(7):127.

Moreno-Opo, R., Trujillano, A., Arredondo, A., González, L. M., and Margalida, A. 2015b. Manipulating size, amount and appearance of food inputs to optimize supplementary feeding programs for European vultures. *Biological Conservation* 181:27–35.

Moreno-Opo, R., Trujillano, A., and Margalida, A. 2016. Behavioural coexistence and feeding efficiency drive niche partitioning at carcasses within the guild of European avian scavengers. *Behavioral Ecology* doi:10.1093/beheco/arw010.

Navarrete A., van Schaik, C. P., and Isler, K. 2011. Energetics and the evolution of human brain size. *Nature* 480:91–93.

Neumann, K. 2009. Bald eagle lead poisoning in winter. In *Ingestion of Lead from Spent Ammunition: Implications for Wildlife and Humans*, ed. R. T. Watson, M. Fuller, M. Pokras, and W. G. Hunt. Boise, ID: Peregrine Fund.

Nikolaus, G. 1984. Large numbers of birds killed by electric power line. *Scopus* 8:42.

———. 2006. Where have all the African vultures gone? *Vulture News* 55:65–67.

Northrup, J. M., and Wittenmeyer, G. 2012. Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. *Ecology Letters*, doi: 10.1111/ele.12009.

Oaks, J. L., Gilbert, M., Virani, M. Z., Watson, R. T., Meteyer, C. U., Rideout, B. A., Shivaprasad, H. L., Ahmed, S., Chaudhry, M. J., Arshad, M., Mahmood, S., Ali, A. and Khan, A. A. 2004. Diclofenac residues as the cause of vulture population decline in Pakistan. *Nature* 427:630–33.

O'Connell, J. F., Hawkes, K., Blurton-Jones, N. 1988. Hadza scavenging: Implications for Plio/Pleistocene hominid subsistence. *Current Anthropology* 29: 356–63.

Ogada, D. L., Keesing, F., and Virani, M. Z. 2012a. Dropping dead: Causes and consequences of vulture population declines worldwide. *Annals of the New York Academy of Sciences* 1249:57–71.

Ogada, D., Shaw, P., Byers, R. L., Buij, R., Murn, C., Thiollay, J. M., Beale, C. M., Holdo, R. M., Pomeroy, D., Baker, N., Kruger, S., Botha, A., Virani, M. Z., Monadjem, A. and Sinclair, A. R. E. 2016. Another continental vulture crisis: Africa's vultures collapsing toward extinction. *Conservation Letters* doi: 10.1111/conl.12182.

Ogada, D. L., Torchin, M. E., Kinnaird, M. F., and Ezenwa, V. O. 2012b. Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. *Conservation Biology* 26:453–60.

Olson, Z. H., Beasley, J. C., DeVault, T. L., and Rhodes, Jr., O. E. 2011. Scavenger community response to the removal of a dominant scavenger. *Oikos* 121:77–84.

Olson, Z. H., Beasley, J. C., and Rhodes, Jr., O. E., 2016. Carcass type affects local scavenger guilds more than habitat connectivity. *PlosOne* 11(2) e0147798.

Oro, D., Margalida, A., Carrete, M., Heredia, R., and Donázar, J. A. 2008. Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. *PLoS ONE* 3:e4084.

Pain, D. J., Cunningham, A. A., Donald, P. F., Duckworth, J. W., Houston, D. C., Katzner, T., Parry-Jones, J., Poole, C., Prakash, V., Round, P., and Timmins, R. 2003. Causes and effects of temporospatial declines of Gyps vultures in Asia. *Conservation Biology* 17:661–71.

Paquet, P. C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. *Journal of Mammalogy* 73:337–43.

Parmenter, R. R., and MacMahon, J. A. 2009. Carrion decomposition and nutrient cycling in a semiarid shrub-steppe ecosystem. *Ecological Monographs* 79:637–61.

Patz, J. A., Epstein, P. R., Burke, T. A., and Balbus, J. M. 1996. Global climate change and emerging infectious diseases. *Journal of the American Medical Association* 275:217–23.

Payne, J. A. 1965. A summer carrion study of the baby pig *Sus scrofa* Linnaeus. *Ecology* 592–602.

Payne, L. X., and Moore, J. W. 2006. Mobile scavengers create hotspots of freshwater productivity. *Oikos* 115:69–80.

Pearson, O. P. 1964. Carnivore-mouse predation: An example of its intensity and bioenergetics. *Journal of Mammalogy* 45:177–88.

Pereira, L. M., Owen-Smith, N., and Moleón, M. 2014. Facultative predation and scavenging by mammalian carnivores: Seasonal, regional and intra–guild comparisons. *Mammal Review*: 44:44-55.

Piper, S. E. 2005. Supplementary feeding programs: How necessary are they for the maintenance of numerous and healthy vultures populations? In *Proceedings of the International Conference on Conservation and Management of Vulture Populations*, ed. D. C. Houston and S. E. Piper, 41–50. Thessaloniki, Greece: Natural History Museum of Crete–WWF Greece.

Putman, R. J. 1976. Energetics of the decomposition of animal carrion. PhD diss., University of Oxford.

———. 1983. *Carrion and Dung: The Decomposition of Animal Wastes*. London: Edward Arnold.

Ragg, J. R., Mackintosh, C. G., and Moller, H. 2000. The scavenging behavior of ferrets (*Mustela furo*), feral cats (*Felis domesticus*), possums (*Trichosurus vulpecula*), hedgehogs (*Erinaceus europaeus*), and harrier hawks (*Circus approximans*) on pastoral farmlands in New Zealand: Implications for bovine tuberculosis transmission. *New Zealand Veterinary Journal* 48:166–75.

Rattner, B. A., Whitehead, M. A., Gasper, G., Meteyer, C. U., Link, W. A., Taggart, M. A., Meharg, A. A., Pattee, O. H., and Pain, D. J. 2008. Apparent tolerance of turkey vultures (*Cathartes aura*) to the non-steroidal anti-inflammatory drug diclofenac. *Environmental Toxicology and Chemistry* 27:2341–45.

Remonti, L., Balestrieri, A., Domensis, L., Banchi, C., Lo Valo, T., Robetto, S., and Orusa, R. 2005. Red fox (*Vulpes vulpes*) cannibalistic behaviour and the prevalence of *Trichinella britovi* in NW Italian Alps. *Parasitology Research* 97:431–35.

Rozen, D. E., Engelmoer, D. J. P., and Smiseth, P. T. 2008. Antimicrobial strategies in burying beetles breeding on carrion. *Proceedings of the National Academy of Sciences* 105:17890–95.

Ruxton, G. D., and Houston, D. C. 2004a. Obligate vertebrate scavengers must be large soaring fliers. *J. Theor. Biol.* 228, 431–36.

Schürenberg, B., Schneider, R., and Jerrentrup, H. 2010. Implementation of recommendation No.110/2004 on minimising adverse effects of above ground electricity transmission facilities (power lines) on birds. Report by the NGOs to the 30th meeting of the Standing Committee of the Bern Convention, Strassbourg. T–PVS/Files (2010) 21. Council of Europe.

Şekercioğlu, C.H. 2006. Ecological significance of bird populations. In *Handbook of the Birds of the World*, vol. 11, ed. J. del Hoyo, A. Elliott, and D. A. Christie, 15–51. . Barcelona and Cambridge: Lynx Press and BirdLife International.

Şekercioğlu, C. H., Daily, G. C., and Ehrlich, P. R. 2004. Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences* 101:18042–47.

Selva, N., and Fortuna, M. A. 2007. The nested structure of a scavenger community. *Proceedings of the Royal Society of London, Series B* 274:1101–8.

Selva, N., Jędrzejewska, B., Jędrzejewski, W., and Wajrak, A. 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Canadian Journal of Zoology* 83:1590–1601.

Shivik, J. A. 2006. Are vultures birds, and do snakes have venom, because of macro- and microscavenger conflict? *BioScience* 56:819–23.

Shultz, S., Baral, H. S., Charman, S., Cunningham, A. A., Das, D., Ghalsasi, G. R., Goudar, M. S., Green, R. E., Jones, A., Nighot, P., Pain, D. J., and Prakash, V. 2004. Diclofenac poisoning is widespread in declining vulture populations across the Indian subcontinent. *Proceedings of the Royal Society London B* 271:S458–S460.

Singer, F. J., Schreier, W., Oppenheim, J., and Garton, E. O. 1989. Drought, fires, and large mammals. *BioScience* 39:716–22.

Smith, C. R., and Baco, A. R. 2003. Ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology* 41:311–54.

Smith, C. R., De Leo, F. C., Bernardino, A. F., Sweetman, A. K., and Martinez Arbizu, P. 2008. Abyssal food limitation, ecosystem structure, and climate change. *Trends in Ecology and Evolution* 23:518–28.

Smith, S., and Paselk, R. 1986. Olfactory sensitivity of the turkey vulture (*Cathartes aura*) to three carrion-associated odorants. *Auk* 103:586–92.

Songserm, T., Amonsin, A., Jam–on, R., Sae-Heng, N., Meemak, N., Pariyothorn, N., Payungporn, S., Theamboonlers, A., and Poovorawan, Y. 2006. Avian influenza H5N1 in naturally infected domestic cat. *Emerging Infectious Diseases* 12:681–83.

Steidl, R. J., Griffin, C. R., and Niles, L. J. 1991. Contaminant levels of osprey eggs and prey reflect regional differences in reproductive success. *Journal of Wildlife Management* 55:601–8.

Swan, G., Naidoo, V., Cuthbert, R., Green, R. E., Pain, D. J., Swarup, D., Prakash, V., Taggart, M., Bekker, L., Das, D., Diekmann, J., Diekmann, M., Killian, E., Meharg, A., Patra, R. C., Saini, M., and Wolter, K. 2006. Removing the threat of diclofenac to critically endangered Asian vultures. *PLoS Biology* 4:396–402.

Swarup, D., Patra, R. C., Prakash, V., Cuthbert, R., Das, D., Avari, P., Pain, D. J., Green, R. E., Sharma, A. K., Saini, M., Das, D., and Taggart, M. 2007. Safety of meloxicam to critically endangered Gyps vultures and other scavenging birds in India. *Animal Conservation* 10: 192–98.

Tabor, K. L., Fell, R. D., and Brewster, C. C. 2005. Insect fauna visiting carrion in Southwest Virginia. *Forensic Science International* 150:73–80.

Tella, J. L. 2001. Action is needed now, or BSE crisis could wipe out endangered birds of prey. *Nature* 410:408.

Tintó, A., Real, J., and Mañosa, S. 2010. Predicting and correcting electrocution of birds in Mediterranean areas. *Journal of Wildlife Management* 74:1852–62.

Towne, E.G. 2000. Prairie vegetation and soil nutrient responses to ungulate carcasses. *Oecologia* 122:232–39.

Vass, A. A. 2001. Beyond the grave: Understanding human decomposition. *Microbiology Today* 28:190–93.

Vass, A. A, Bass, W. M., Wolt, J. D., Foss, J. E., and Ammons, J. T. 1992. Time since death determinations of human cadavers using soil solution. *Journal of Forensic Science* 37: 1236–53.

VerCauteren, K. C., Pilon, J. L., Nash, P. B., Phillips, G. E., and Fischer, J. W. 2012. Prion remains infectious after passage through digestive system of American crows (*Corvus brachyrhynchos*). *PLoS ONE* 7:e45774.

Weaver, D. B. 2008. *Ecotourism*. Milton, Australia: John Wiley & Sons.

Wilmers, C. C., Crabtree, R. L., Smith, D. W., Murphy, K. M., and Getz, W. M. 2003b. Trophic facilitation by introduced top predators: Grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology* 72:909–16.

Wilmers, C. C., and Post, E. 2006. Predicting the influence of wolf-provided carrion on scavenger community dynamics under climate change scenarios. *Global Change Biology* 12:403–9.

Wilmers, C. C., Stahler, D. R., Crabtree, R. L., Smith, D. W., and Getz, W. M. 2003a. Resource dispersion and consumer dominance: Scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. *Ecology Letters* 6:996–1003.

Wilson, E. E., and Wolkovich, E. M. 2011. Scavenging: How carnivores and carrion structure communities. *Trends in Ecology and Evolution* 26:129–35.

Wormworth, J., Şekercioğlu, C. H. 2011. *Winged Sentinels: Birds and Climate Change*. Cambridge University Press, New York.